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The life-history of *Caleta roxus* (Lepidoptera: Lycaenidae)

by

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Abstract: *Caleta roxus* (GODART [1824]) lays its yellow eggs singly on young shoots of a climber in the family Rhamnaceae. Larvae hatch after 4–5 d. Caterpillars feed on young foliage. There are 4 larval instars, larval development lasts 22 d. The green caterpillars are very flat and hairy. L_3 and L_4 larvae have a yellow middorsal band. Caterpillars lack a dorsal nectary organ and tentacle organs and are not attended by ants. The girdled pupae are likewise hairy and are not attractive to ants. The butterfly emerges after a pupal period of 8 d. Both larvae and pupae are able to produce substrate-borne vibrations when disturbed. The observations on *C. roxus* are discussed with respect to phylogenetic and ecological implications.

Zur Biologie von *Caleta roxus* (Lepidoptera: Lycaenidae)

Zusammenfassung: Beobachtungen zur Biologie von *Caleta roxus* (GODART [1824]) in Westmalaysia werden beschrieben. Die männlichen Falter saugen gerne an feuchter Erde, Vogelkot o. ä., beide Geschlechter besuchen Blüten. Die Eiablage erfolgt einzeln in der Mittagszeit an jungen Blättern und Ranken einer Liane (Familie Rhamnaceae, eine genauere Bestimmung war mangels Blüten bislang unmöglich). Aus den gelben Eiern (Durchmesser 0,5 mm) schlüpfen nach 4–5 Tagen die Jungraupen. *C. roxus* hat 4 Larvenstadien. Als Futter dienen junge Blätter, die Raupen fressen im Freiland tagsüber, in der Zucht auch nachts. Die Verpuppung erfolgt nach ca. 22 Tagen, der Falter schlüpft nach weiteren 8 Tagen. Die Raupen sind im Vergleich zu anderen Polyommatini-Larven sehr flach und haarig. Ihre Grundfarbe ist grün, in den beiden letzten Stadien tragen sie einen deutlichen gelben Längsstreifen auf der Rückenmitte. Vor der Verpuppung verfärben sich die Raupen rötlich. Die Gürtelpuppe ist ebenfalls recht flach, lang behaart, bräunlich mit dunkleren Punkten. Raupen und Puppen von *C. roxus* sind im Freiland wie im Labor myrmekoxen, auch die Eiablage erfolgt ohne Ameisen. Den Raupen fehlen ein dorsales Nek-

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tarorgan wie auch die Tentakelorgane. Dennoch sind Raupen und Puppen bei Störung zur Produktion substratgetragener Vibrationssignale fähig. Die innerhalb der Polyommatini recht seltene Bindung an die Wirtspflanzenfamilie Rhamnaceae teilt *C. roxus* mit 3 weiteren Arten der *Upolampes*-Sektion. Die mögliche Bedeutung dieser Rhamnaceen-Bindung im Hinblick auf die Verwandtschaft mit anderen Polyommatini (*Castalius*- und *Danis*-Sektion) wird diskutiert. Abschließende Bemerkungen gelten der Evolution sekundärer Myrmekoxenie in tropischen, außerordentlich ameisenreichen Habitaten.

The Polyommatini genus *Caleta* FRUHSTORFER [1922] comprises small, delicately black-and-white coloured lycaenid butterflies (Fig. 1), which occur in the Oriental region from India to New Guinea. On the grounds of studies of type material by TAKANAMI (1989) and his own studies of genitalia morphology, HIROWATARI (1992) recognizes 9 species (BRIDGES 1988 lists only 5 valid species along with numerous infraspecific taxa). Together with *Discolampa* TOXOPEUS 1929 (3 Oriental species) and the monotypic New Guinean genera *Pistoria* HEMMING 1964 and *Upolampes* BETHUNE-BAKER 1908, the 4 genera constitute the *Upolampes* section sensu HIROWATARI (1992). The phylogenetic affinities of this small section (14 species) are poorly known. Superficially, the species resemble members of the *Castalius* section (included genera: *Castalius* HÜBNER [1819], *Tuxentius* LARSEN 1982, *Tarucus* MOORE [1881], *Zintha* ELIOT 1973), and most species of *Caleta* and its related genera have indeed long been included in *Castalius*. Because of major genitalic differences, but without presenting a phylogenetic reasoning, ELIOT (1973, 1992) as well as HIROWATARI (1992) treat the two sections as separate entities. However, larval hostplant associations may indicate a closer relationship. Caterpillars of *Castalius, Tuxentius, Tarucus* and *Zintha* feed on Rhamnaceae (rarely on additional plant families: FIEDLER 1991). The few available hostplant records for *Caleta decidia* (HEWITSON [1876]), *C. elna* (HEWITSON [1876]) and *Discolampa ethion* (WESTWOOD [1851]) (see FIEDLER 1991, ELIOT 1992) are also from the Rhamnaceae.

Here I report on the hitherto unknown biology of another species, *Caleta roxus* (GODART [1824]). Most observations were conducted in August and September 1992 in the vicinity of the Ulu Gombak Field Studies Centre of the Universiti Malaya (Peninsular Malaysia). Supplementary observations were made at various other times between 1988 and 1993 at the same locality. The study area largely consists of

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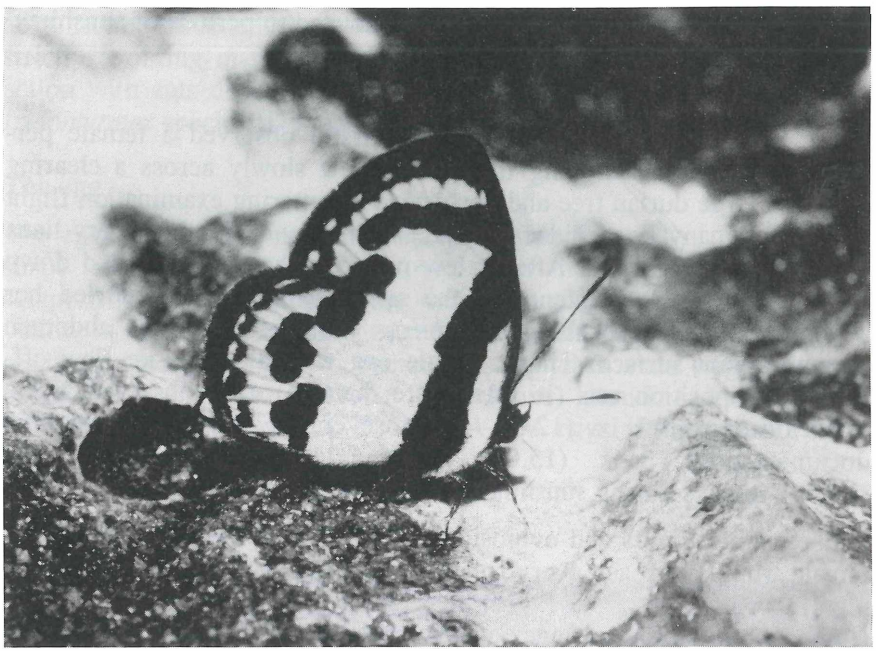

Fig. 7: Male *Caleta roxus* puddling at a bird dropping (Gombak valley, April 1993).

advanced secondary rain forest of the lowland dipterocarp type, and is located in the Gombak valley about 20 km northwest of the Malaysian capital Kuala Lumpur at an elevation of 200–400 m. The populations on the Malay Peninsula can be referred to as *C. roxus pothus* (FRUHSTORFER 1918).

Adult behaviour

Male *Caleta roxus* butterflies can often be observed puddling at moist river banks or on bird droppings (Fig. 7). At such mineral sources, several males may be found simultaneously, often together with other butterflies (e.g., *Actyolepis puspa* (HORSFIELD [1828]) or the pierid genus *Eurema* HÜBNER [1819]). Males as well as females also visit flowers, mostly weedy herbs along sunny roadsides. Recorded nectar sources include *Stachytarpheta jamaicensis* (Verbenaceae) and *Hyptis brevipes* (Lamiaceae; both species introduced to Malaya from the

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Neotropics: HENDERSON 1974), but the list of nectar-plants is certainly much longer. Flight activity is largely restricted to periods of sunshine.

Oviposition

On 1. ix. 1992, 13.00 h local time, I firstly observed a female performing a typical searching flight. She flew slowly across a clearing around a large durian tree and performed a fluttering examination flight typical for many Lycaenidae butterflies, thereby examining every liana 0.3–1 m above ground. After a few minutes, the female settled down on a peculiar plant, antennated the substrate intensively, curled her abdomen and made probing movements with the tip of the abdomen over the plant surface. Then a single egg was laid and she flew off. Further oviposition acts (in total more than 15) were observed at the same location on 2. ix. (12.30–13.30, several eggs laid, photographic documentation), 3. ix. (15.00), 13. ix. (15.00), and 14. ix. 1992 (13.00), always during sunshine or slightly overcast weather.

All searching flights and oviposition acts followed the same pattern. A female would approach every free end of a liana or twig, irrespective of plant species, but rarely higher than 1 m above ground. Then, while slowly fluttering at a distance of less than 2 cm to the plant, she would decide whether or not to alight. Alighting invariably occurred on the true hostplant only, except when a female butterfly landed to rest in the vegetation, sitting in an upright position with closed wings. After alighting on the hostplant, the substrate would be thoroughly investigated using the antennae first and the abdominal tip subsequently. Finally, a single egg would be deposited. The whole procedure suggests that host searching behaviour in *C. roxus* starts with looking for plants that match a visual search image, followed by olfactory examination based on volatile and later surface chemicals of the hostplant, using chemo- and mechanoreceptors of the antennae and ovipositor.

Eggs were deposited only on one plant species: a woody climber in the family Rhamnaceae. Due to the lack of flowers or seeds, a precise determination is yet impossible, but following KENG (1983) the plant belongs to either *Ventilago* or *Smythea* (unfortunately an attempt to receive a meaningful generic determination through the help of the Forest Research Institute of Malaya, Kepong, failed). The hostplant is locally common in the Gombak valley and occurs on small forest clearings (like the 1992 observation site), along rivers and roadsides,

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always in sun-exposed positions. Eggs are laid on young leaves (preferably on the undersides) or on terminal parts of the climbing shoots, strictly avoiding mature foliage. On no occasion was there any interaction with ants during oviposition, although foraging ants (mostly an *Iridomyrmex* species [Dolichoderinae]) regularly patrolled the hostplant.

The egg

The eggs are ca. 0.5 mm in diameter, rather flat and of the disc-like shape of many Polyommatini ova. They have a rough chorionic sculpturing (Fig. 8). Shortly after oviposition, eggs of *Caleta roxus* are yellow in colour. Later the eggs turn into white, and when the larva is ready to hatch, the eggs become dark. In glass vials under ambient conditions (temperature 22–28 °C, relative humidity > 90 %) the caterpillars hatched after 4–5 days. A few eggs were parasitized by minute unidentified hymenopterans.

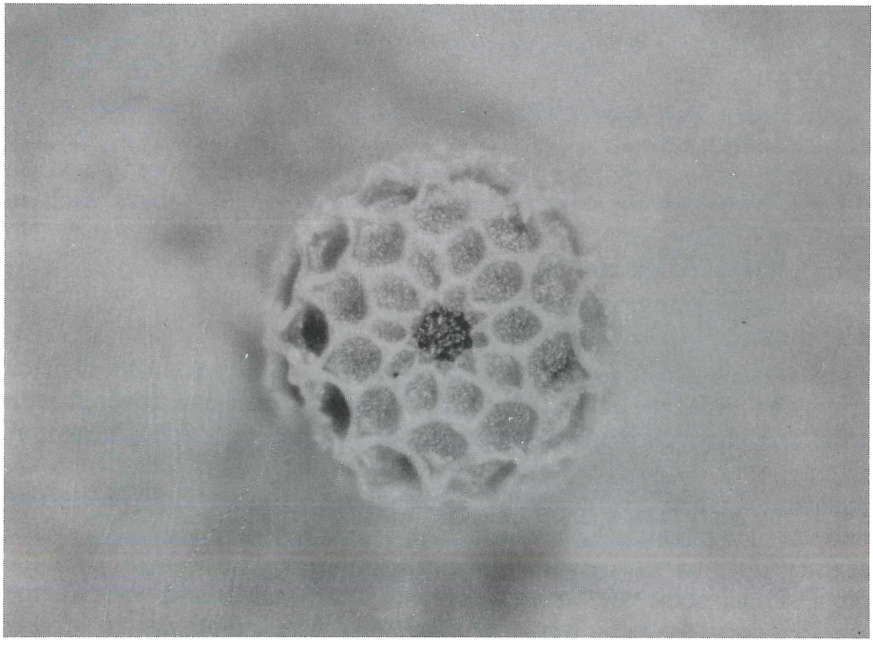

Fig. 8: Egg of *C. roxus*. Diameter = 0.5 mm.

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The larva

Caleta roxus has four larval instars. First and second instars are light green, with only a faint yellowish dorsal midline (Fig. 2). From the third instar onwards, the larvae are darker green and bear a pair of yellowish parallel middorsal lines, which range from the second thoracic segment to the eighth abdominal segment (Fig. 4). The spiracles are inconspicuously light green. The caterpillars are remarkably flat (Fig. 9), resembling the larvae of certain hairstreaks (e.g. *Arhopala* BOISDUVAL 1832) rather than many Polyommatini caterpillars. They are densely covered with numerous setae. Particularly long, erect bristles are found along the lateral margins of the larvae, whereas on the dorsum the hairs are shorter and more curved. All these setae are inserted in stellate chalazae and have spiny hair shafts. The overall appearence of the caterpillars is unusally "fuzzy" as compared with most other Polyommatini larvae. Pore cupola organs with stellate chalazae occur scatteredly in small numbers among the short, curved setae of the dorsum. *C. roxus* larvae possess neither a dorsal nectary organ nor a pair of tentacle organs.

Larval development was comparatively slow. Five caterpillars sampled in the field as late second and early third instars on 1. ix. 1992 pupated on 15.–17. ix. in captivity, passing an immobile prepupal stage of about 1 day duration. When the larvae stopped feeding, their green ground colour turned reddish (Fig. 5) and they searched for a pupation site. In captivity they preferably pupated on leaves or, more rarely, on filter paper. The first and second instar took about 4 days each in captivity, adding up to a total larval period of roughly 22 days. No parasitoids were reared from the field-collected larvae.

The pupa

Caleta roxus pupae are attached to the substrate with a girdle and the cremaster. Like the larva, the pupa is relatively flat and covered with stiff, long bristles (Fig. 6). Pupal ground colour is a light brown. A reddish brown mid-dorsal line extends from the second thoracic to the eighth abdominal segment. A supraspiracular row of dark dots (one pair per segment) extends from the second to seventh abdominal segments. Otherwise, small dark dots are found irregularly all over the pupa. Pupal setae are long, erect with spiny hair shafts. Unlike the larval instars, the pupa has large clusters of pore cupola organs around the abdominal spiracles and immediately anterior of the prothoracic

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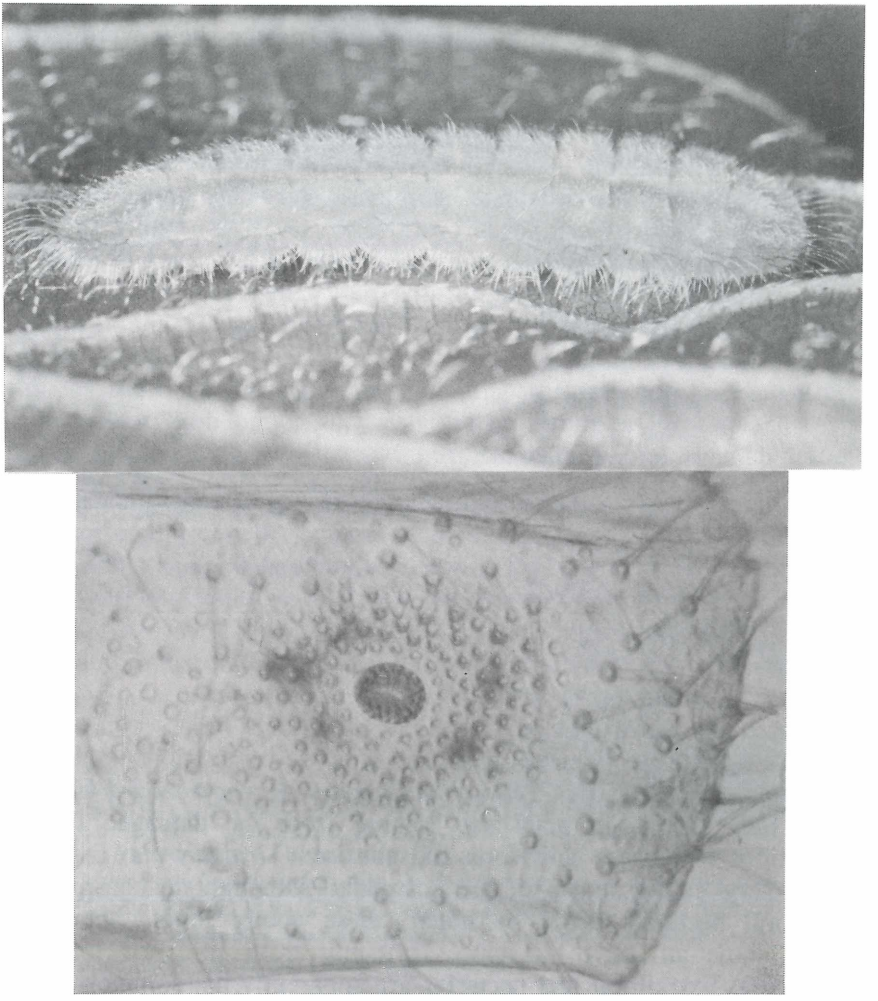

Fig. 9 (top): Mature caterpillar of *C. roxus* in profile. The larva is unusually flat. Length 12 mm.
Fig. 10 (below): Group of pupal pore cupola organs around an abdominal spiracle.

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spiracle (Fig. 10). A stridulatory organ of the usual type is present at the contact zone between abdominal segments 5/6. No parasitoids emerged from the pupae. Pupal development took 8 days (n = 6).

Feeding behaviour, relationship to ants, and call production

Young larvae (up to the third instar) feed by making holes in young leaves of their hostplant. Although most eggs or egg-shells were found on the undersides of the leaves, larvae were observed feeding on both sides of the leaves in approximately equal numbers. Older larvae (L_3 & L_4) were only found on the uppersides. Fourth instars fed on the whole leaves (Fig. 3). Feeding occurred during daytime in the field, but continued at night in captivity under ambient conditions, suggesting that there may be no distinct diurnal cycle. The larvae (especially final instars) showed a peculiar defecation behaviour. A larva would bend its rear end upwards before expelling the frass pellet (Fig. 3). Hence, all frass falls to the ground instead of accumulating on the hostplant leaves, where it could attract parasitoids or predators. The same defecation behaviour was performed in captivity. Cannibalism occurred only once in captivity: a fourth instar larva was found dead with typical feeding damage among other mature larvae.

Caterpillars of *C. roxus* are myrmecoxenous, as already indicated by the lack of a nectary organ and tentacle organs. All caterpillars found in the field (11 $L_{1/2}$, 9 L_3, 1 L_4) were unattended by ants. The larval habitat was highly dominated by an *Iridomyrmex* species whose workers foraged on practically all plants in the lower part of the vegetation. However, only one contact between *Iridomyrmex* ants and a *C. roxus* L_3 could be observed. In this encounter, one ant passingly antennated the larva and left it unharmed after a few seconds. The butterfly eggs were likewise ignored. Ants were occasionally seen at fresh feeding marks of *C. roxus* caterpillars or chrysomelid beetles, where they licked up plant sap issuing from the damaged leaves. Interactions with these herbivores did not occur. *Iridomyrmex* ants also visited very young shoots of the hostplant. Although no conspicuous extrafloral nectaries could be noted, these young shoots appear to secrete some attractive substance (possibly from so-called formless nectaries?). Extrafloral leaf nectaries are apparently not common in the Rhamnaceae, but have been documented in that plant family (KOPTUR 1992).

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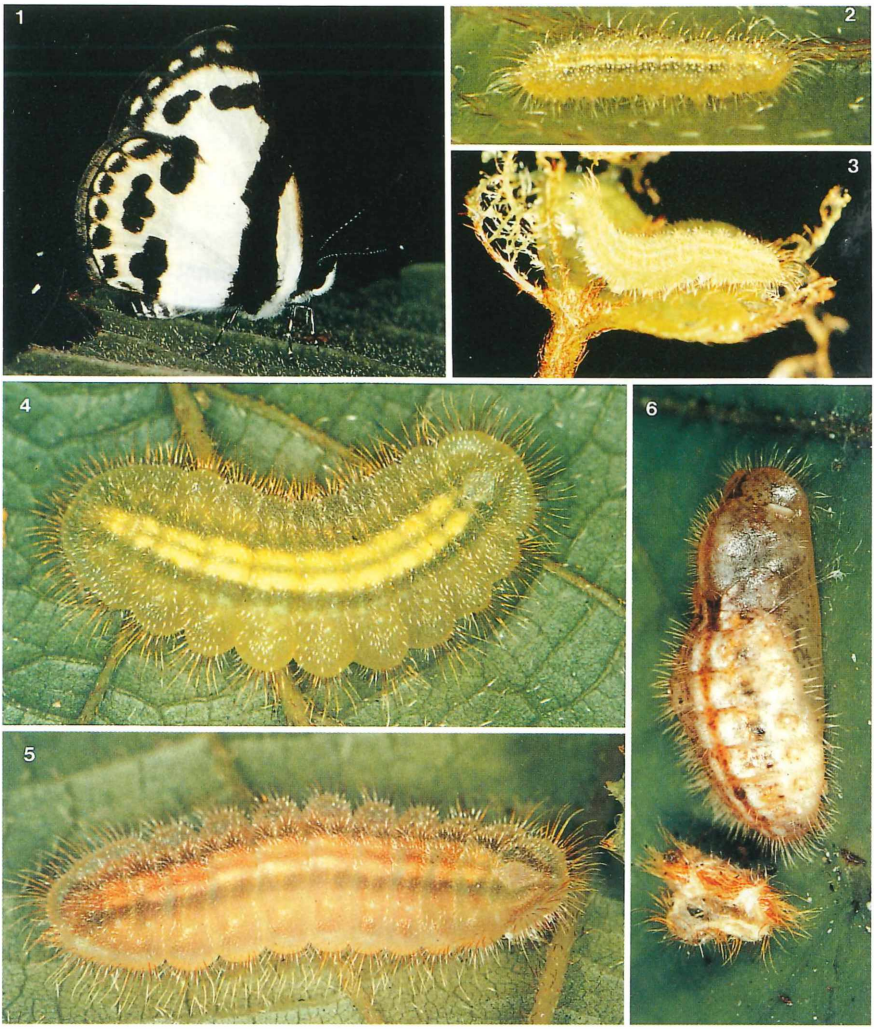

Fig. 1–6 (colour plate): *Caleta roxus*. **Fig. 1:** Freshly emerged butterfly. **Fig. 2:** Second instar larva (length 5 mm). **Fig. 3:** Fourth instar larva, defecating with rear end bent upwards. **Fig. 4:** Mature larva, length 12 mm. Note strong hairiness of the myrmecoxenous caterpillar. **Fig. 5:** Caterpillar in prepupal stage. Note reddish colour. **Fig. 6:** Pupa. Note conspicuous girdle and long hairs.

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In captivity, L_3 and L_4 larvae of *C. roxus* were confined with *Iridomyrmex* ants from the original habitat as well as with another trophobiotic ant species known to attend lycaenid caterpillars in nature, viz. *Rhoptromyrmex wroughtonii* (Myrmicinae). Both ant species ignored the caterpillars and never attempted to attack. With *Rh. wroughtonii,* a total of only 5 intensive antennation acts could be observed in two periods of 7 or 8 days, respectively. On these occasions, a single *Rh. wroughtonii* worker antennated a caterpillar for 10–20 seconds on the dorsum of the seventh abdominal segment (i.e., the location where myrmecophilous larvae bear the nectary organ), then left. As in the field, *Iridomyrmex* ants never paid any attention to *C. roxus* larvae over a 4 d period in a plastic rearing box. Despite their large numbers of pore cupola organs, pupae were likewise ignored by ants. I could not observe any single interaction between *Rh. wroughtonii* and *C. roxus* pupae over a test period of 7 days.

Like many other lycaenid caterpillars (DEVRIES 1991a), larvae of *C. roxus* are able to produce substrate-borne vibrations. These calls were recognized in L_3 and L_4 larvae by use of a stethoscope (SCHURIAN & FIEDLER 1991). One second instar did not call when tested. The calls were of low amplitude and not easy to detect. In addition, the readiness to vibrate after tactile disturbance varied greatly between individuals and days. In 2 out of 3 trials with L_3 larvae, and in 7 out of 12 trials with fourth instars could calls be recognized. Calling occurred only immediately during and after tactile disturbance with forceps and never lasted for more than a few seconds. Calls consisted of short pulses, the auditory impression to the human observer was a faint croaking or snarling noise. Only one L_3 caterpillar produced calls that consisted of two different frequency components (a low-frequency rustling base component in addition to the croaking sound).

Although pupae of *C. roxus* possess what appears to be a "stridulatory organ", pupal stridulations were never recognized. On only one occasion (out of 15 tests on the stethoscope) I perceived a faint rustling vibratory signal produced by a pupa whose eyes were already pigmented. This pupa had previously been molested very heavily with forceps. The chirping (and partly air-borne) sounds so typical for many Lycaenidae pupae were never heard.

Discussion

In short, *Caleta roxus* can be characterized as a tropical lycaenid butterfly with a hostplant in the Rhamnaceae, whose hairy larvae and

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pupae are myrmecoxenous with limited abilities to emit substrate-borne vibrations. The hostplant relationship of *C. roxus* well matches what is known about its closest relatives: *C. elna, C. decidia* and *Discolampa ethion* all feed on Rhamnaceae (mainly on *Zizyphus*). A strong Rhamnaceae association is also characteristic for the *Castalius* section (hostplants known for 22 species) as well as for the *Danis* section (genera *Danis* FABRICIUS 1807 and *Psychonotis* TOXOPEUS 1930, hostplants known for one member each; cf. FIEDLER 1991). Taken together the members of these three Polyommatini sections account for 53 % of all lycaenids known to feed on Rhamnaceae (28 out of 53 species). Within the Polyommatini, only the highly polyphagous caterpillars of *Celastrina argiolus* (LINNAEUS 1758) and *C. ladon* (CRAMER [1780]) have additionally been recorded from Rhamnaceae. Hence, specialization on Rhamnaceae appears to be a rare event among Polyommatini lycaenids, and their common hostplant association (on family level) might suggest a closer phylogenetic affinity between the *Discolampa, Castalius* and *Danis* sections.

Further support for this idea comes from some similarities of the caterpillars. Larvae of Mediterranean and African members of the *Castalius* section are mostly flat, and in one species (*Tuxentius melaena* (TRIMEN 1887)) there is a similar lateral fringe of stiff bristles as in *Caleta roxus* (CLARK & DICKSON 1971). COMMON & WATERHOUSE (1981) describe the caterpillar of the Australian *Psychonotis caelius* (C. & R. FELDER 1860) (under the name *"Danis hymetus* (C. FELDER 1860)", see HIROWATARI 1992) as flat and rather hairy, but unfortunately no figure is given. In contrast to many other Polyommatini larvae that strongly prefer inflorescences as food, the caterpillars of *Caleta, Castalius, Tuxentius, Tarucus, Zintha, Danis* and *Psychonotis* are all reported to feed on leaves. This would well explain their external appearance: flat caterpillars matching their hostplants in colour are perfectly camouflaged. It remains to be ascertained in the course of a strictly phylogenetic analysis whether the above similarities in hostplant use and larval morphology are the result of convergent colonization of the Rhamnaceae as hostplants, or are indicative of common ancestry.

As far as yet known, the caterpillars of all members of the *Castalius* section are myrmecophilous and possess a full set of related glandular organs. Some *Tarucus* species even have a very close (and possibly obligatory) association with *Crematogaster* ants (see references in FIEDLER 1991). In the *Danis* section, information concerning myr-

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mecophily is scant. BALLMER & PRATT (1988) report the presence of a DNO and absence of TOs in *Psychonotis hymetus,* but like in *Danis danis* (CRAMER [1775]), ant-associations appear to be unrecorded (COMMON & WATERHOUSE 1981). In the *Upolampes* section, the situation is again different. Myrmecophilous organs are definitively absent in *Caleta roxus* (see above) and *Discolampa ethion* (HINTON 1951), and both species are not tended by ants in nature. For *C. elna* only the hostplant has been recorded (ELIOT 1992). Surprisingly, *Caleta decidia* is said to be facultatively attended by ants and to possess a DNO plus TOs (HINTON 1951, citing BELL's observations from India). Assuming that these observations on *C. decidia* are correct, the question arises as to how often myrmecophily has been lost in the *Upolampes* section.(1) Either has myrmecophily been lost twice independently in the lineages that later gave rise to the species *C. roxus* and *D. ethion*. Alternatively, the loss of myrmecophily has occurred only once in the group in question. This would require a rearrangement of the present generic subdivision. As pointed out by HIROWATARI (1992), there is some heterogeneity in what is today called *"Caleta"*. Clearly, detailed biological observations on further species, including confirmatory records on species already known, are required to solve that problem.

The selective forces promoting reductions of myrmecophily within the Lycaenidae are generally not well understood (see FIEDLER 1991 for discussion). In *Caleta roxus* this is particularly difficult to understand, since the species occurs in tropical rainforest habitats with a very high abundance and diversity of ants. However, the caterpillars are well adapted to co-exist with these ants without being prone to ant-predation. Besides their few pore cupola organs the quite long hairs might confer some protection against ant attacks. As pointed out by DEVRIES (1991b), "fuzzy" caterpillars of Lycaenidae and Riodinidae are generally myrmecoxenous. Further cases of secondary myrmecoxeny are now known for an increasing number of tropical Lycaenidae species (e.g., *Cheritra freja* (FABRICIUS 1793), SEUFERT & FIEDLER, unpublished). If secondary myrmecoxeny were more widespread among tropical lycaenids, this would further challenge the hypothesis that ant-associations of Lycaenidae butterflies are generally more common and

(1) = Because myrmecophily with its related organs is almost universally present in all major lineages of the Polyommatini, the scattered occurrence of myrmecoxeny is most parsimoniously explained as an apomorphic character state within that tribe of the Lycaeninae at least (FIEDLER 1991).

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more close in tropical and subtropical faunas than in the Northern hemisphere (PIERCE 1987; see FIEDLER in press).

Caleta roxus is yet another lycaenid species whose larvae are myrmecoxenous, but are capable of producing vibratory calls. Further examples of calling, myrmecoxenous caterpillars are found in various species of *Lycaena* FABRICIUS 1807, in *Callophrys rubi* (LINNAEUS 1758), at least in two species of *Curetis* HÜBNER [1819] and in *Cheritra freja* (SCHURIAN & FIEDLER 1991, FIEDLER & SEUFERT, unpublished). Although the vibratory abilities of *C. roxus* caterpillars and pupae are weakly developed, these observations again challenge the hypothesis of DEVRIES (1990, 1991a) that, within the Lycaenidae, call production is confined to myrmecophilous species and acts as additional means of butterfly-ant communication. The biological significance of call production remains to be thoroughly tested for various lineages of the Lycaenidae.

In summary, the observations reported here not only document the life-history of *Caleta roxus*. In a comparative context, they also pose interesting questions concerning the higher classification, generic taxonomy, evolutionary biology and behavioural ecology of lycaenid butterflies. This exemplifies the importance of detailed descriptive accounts on the biology of many more individual species, especially from the highly speciose tropical regions. Without such descriptive work, there is little basis for further analytical research.

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